### **Gulf and Caribbean Research**

Volume 19 | Issue 1

January 2007

## Breeding Season and Molt Cycle of the Fiddler Crab *Uca rapax* (Brachyura, Ocypodidae) in a Subtropical Estuary, Brazil, South America

Daniela da Silva Castiglioni Instituto de Biociencias, Brazil

Maria Lucia Negreiros-Fransozo Instituto de Biociencias, Brazil

Rosana Carina Flores Cardoso Instituto de Biociencias, Brazil

Follow this and additional works at: https://aquila.usm.edu/gcr



#### **Recommended Citation**

da Silva Castiglioni, D., M. Negreiros-Fransozo and R. C. Flores Cardoso. 2007. Breeding Season and Molt Cycle of the Fiddler Crab *Uca rapax* (Brachyura, Ocypodidae) in a Subtropical Estuary, Brazil, South America. Gulf and Caribbean Research 19 (1): 11-20. Retrieved from https://aquila.usm.edu/gcr/vol19/iss1/2 DOI: https://doi.org/10.18785/gcr.1901.02

This Article is brought to you for free and open access by The Aquila Digital Community. It has been accepted for inclusion in Gulf and Caribbean Research by an authorized editor of The Aquila Digital Community. For more information, please contact aquilastaff@usm.edu.

### BREEDING SEASON AND MOLT CYCLE OF THE FIDDLER CRAB UCA RAPAX (BRACHYURA, OCYPODIDAE) IN A SUBTROPICAL ESTUARY, BRAZIL, SOUTH AMERICA

# Daniela da Silva Castiglioni, Maria Lucia Negreiros-Fransozo\*, and Rosana Carina Flores Cardoso

(MLNF; RCFC) NEBECC (Group of Studies on Crustacean Biology, Ecology and Culture), Departamento de Zoologia, Instituto de Biociências, Caixa Postal 510, UNESP, 18618-000, Botucatu, São Paulo, Brasil; (DSC) Graduation Course in Zoology, Instituto de Biociências, UNESP, Botucatu, São Paulo, Brasil \*Corresponding author. E-mail mlnf@ibb.unesp.br

ABSTRACT This is the first account of the breeding season and molt cycle of Uca rapax on the Brazilian coast during a one-year period (April 2001–March 2002). At 2 sites, the Itamambuca and Ubatumirim mangrove forests, 2 collectors captured crabs once a month at low tide for 15 minutes by the catch-per-unit-effort procedure, digging into the sediment and removing the crabs. The gonad-development stages of crabs of both sexes were determined by direct observation, and the molt stage was estimated from the hardness of the tegument. Crabs with developed gonads were found mostly in warmer seasons, with ovigerous females occurring mainly in summer and autumn. The reproductive cycle is seasonal. Recently molted individuals were collected in relatively higher numbers for juveniles than for adult crabs.

#### INTRODUCTION

The reproductive strategy of brachyuran crabs is extremely diversified, ultimately shaped to maximize egg production and offspring survivorship, thus increasing the chances for preservation of the species (Hartnoll and Gould 1988). The reproductive period for many brachyurans can be estimated by observing gonad maturation at the macro- or microscopic levels and from the frequency of ovigerous females in the population (e.g., Wolfrath 1993, Emmerson 1994, Mouton and Felder 1995, Costa and Negreiros-Fransozo 2003, Colpo and Negreiros-Fransozo 2003, Litulo 2004, 2005a, 2005b). The reproductive period results from a complex interaction between internal and external factors, leading to intra- and inter-specific variation in the duration of the reproductive season (Sastry 1983).

Many ocypodid crabs have seasonal reproduction, as observed in Uca lactea (de Haan, 1835) studied by Yamaguchi (1971), in Uca pugilator (Bosc, 1802) and Uca pugnax (Smith, 1870) studied by Christy (1982), and Uca thayeri Rathbun, 1900 studied by Salmon (1987). The limited reproductive season in semi-terrestrial crabs might be related to changes in the temperature and photoperiod and the availability of food resources (Pillay and Ono 1978). The availability of food for body maintenance, somatic growth and reproduction of the adult crabs, and for growth and survival of the larval and/or juvenile stages is assumed to be the most important factor (Sastry 1983) in synchronization and coordination of reproductive activity in a given habitat.

Mangrove ecosystems are highly productive environments, hospitable for feeding, growth, and reproduction of many species of crabs, shrimps, fishes, and other animals (Schaeffer-Novelli 1995). In these ecosystems, fallen mangrove leaves provide most of the organic matter deposited in the sediments. Deposit-feeding ocypodid crabs of the genus Uca feed on the organic matter, including the endofauna that are sorted out from the substrate. Their actual food supply depends on the ecosystem productivity, microbial activity, substrate texture, and tidal action (Murai et al. 1982, Twilley et al. 1995, Moura et al. 1998). There are about 100 species of fiddler crabs worldwide, most of them included in 2 distinct morphological categories with different morphology, zoogeography, and behavior: the broad-front species and the narrow-front species (Crane 1975, Christy and Salmon 1984, Rosenberg 2001). There are about 10 species of fiddler crabs typically found in Brazilian mangroves: Uca burgersi Holthuis, 1967; Uca cumulanta Crane, 1943; Uca leptodactyla Rathbun, 1898; Uca mordax (Smith, 1870); Uca rapax (Smith, 1870); Uca uruguayensis Nobili, 1901; Uca victoriana (von Hagen, 1987); Uca vocator (Herbst, 1804); Uca thayeri Rathbun, 1900; and Uca maracoani (Latreille, 1802-1803) (Melo 1996). A peculiar morphological feature separating these species into 2 groups is the size of the carapace front. Uca burgersi, U. cumulanta, U. leptodactyla, U. mordax, U. rapax, U. uruguayensis, U. victoriana, U. vocator and U. thayeri have a broad front, while U. maracoani has a narrow front.

Among the species studied here, U. rapax is one of the most abundant species of the genus Uca in the Brazilian

mangroves. It burrows into mud or muddy sand and feeds on organic matter in the sediment of mangroves along the northern coast of the State of São Paulo, Brazil. According to Melo (1996), *U. rapax* is distributed throughout Florida, the Gulf of Mexico, the Antilles, Venezuela, and Brazil (from the states of Pará to Santa Catarina).

This study investigates the breeding season and molt cycle of U. rapax from the Itamambuca and Ubatumirim mangrove forests near Ubatuba on the northern coast of São Paulo, Brazil. The studies are based on the frequency of gonad and molt stages and the ratio of ovigerous females. Although located close to each other, the study sites have distinct landscapes and hydrological features that determine the vegetation community. The vegetation in the Itamambuca mangrove (23°24'4"S, 45°00'7"W) consists of only Laguncularia racemosa (Linnaeus). In the Ubatumirim mangrove (23°20'17.8"S, 44°53'22"W) the vegetation is mostly L. racemosa with some Avicennia shaueriana Stapf. and Leech (Negreiros-Fransozo, pers. comm.). The Itamambuca mangrove is a highly productive ecosystem with hydrology and sediment characteristics that retain minerals and a rich environment suitable for development of fiddler crab populations (Colpo 2001). As described by Castiglioni and Negreiros-Fransozo (2004), these 2 mangroves have distinctly different sediment organic matter content and texture as well as river and burrow salinities.

#### MATERIAL AND METHODS

Crabs were collected monthly by 2 people from April 2001 through March 2002 in both mangroves, using the procedure of catch per unit effort (cpue). Over 15 min time periods during low tides (spring tide), crabs were removed from their burrows by digging to the end of each burrrow with diving knives. Additional collections were made in August through December 2002, using the same procedure attempting to locate ovigerous females.

Crabs were counted, sexed, and measured (carapace width (CW) to the nearest 0.01 mm), and females were checked for eggs. Ovigerous females were preserved individually in 70% ethanol.

We determined the relative frequency of ovigerous females over the course of the year. The stages of embryonic development were classified as initial, intermediate, or final, according to the relative proportion of yolk content and the appearance of eyes and appendage buds in the embryo (see Costa and Negreiros-Fransozo 1998 for details). A multinomial proportions analysis (Curi and Moraes 1981) with a 5% significance level was used to examine reproductive seasonality. From this analysis we considered autumn as April, May, and June; winter as July, August, and September; spring as October, November, and December; and summer as January, February, and March.

The size of ovigerous females was compared between the populations by Student's t test ( $\alpha = 0.05$ ; Zar 1996). The gonad development stages were analyzed in each sex. The carapace in the dorsal region was removed, and the shape, size, and color of the gonads were observed under a stereomicroscope. The female gonads were classified in 6 developmental stages: spent = SP; advanced = AD; developed = DE; developing = DI; rudimentary = RU; and immature = IM. Five stages were used for males: spent = SP; developed = DE; developing = DI; rudimentary = RU and immature = IM. This procedure was modified from Haefner (1976), Abelló (1988), Choy (1988) and Costa and Negreiros-Fransozo (1998). Comparisons of the gonad proportion between seasons in each sex were performed using a multinomial proportions analysis (Curi and Moraes 1981) to determine the reproductive period.

Fiddler crabs were arranged in 2 groups: juvenile or immature crabs (specimens with immature or rudimentary gonads) and adult or mature crabs (specimens with developing, developed, advanced, or spent gonads). Comparisons of the immature and mature crabs between seasons in each sex were performed using a multinomial proportions analysis (Curi and Moraes 1981). The reproductive period was determined using data for the frequency of mature males and females over the year (Costa and Negreiros-Fransozo 1998, Mantelatto and Fransozo 1999).

The air and burrow temperatures were measured monthly, with 3 replicates at each site, and were compared by ANOVA among seasons and sites ( $\alpha = 0.05$ ; Zar 1996). The degree of association among crabs with developed gonads and environmental factors (air and burrow temperatures) was assessed using Pearson's correlation ( $\alpha = 0.05$ ; Zar 1996).

The molt stages were described based on Warner (1977) and Abelló (1988) as follows: A) post-recent molt = carapace very flexible and without calcification; B) post-advanced molt = onset of calcification; brittle carapace but more resistant and with a consistency similar to cardboard; C) intermolt = carapace fully calcified, with a leathery consistency; D) pre-molt = a new exoskeleton present inside the old one and the molt lines emerging in the pterigostomial region; and E) molt = exact moment of the change or exit of the animal from the old exoskeleton.

Following this scheme, the molt stages were grouped in 2 phases: molt activity (A, B, and D stages) and intermolt (C stage). The proportions of the 2 stages were compared between seasons using the multinomial proportions analysis (Curi and Moraes 1981). We analyzed the molt frequency in each sex by size class (CW) for both mangroves.

#### RESULTS

During the study period, a total of 1,294 fiddler crabs were collected at Itamambuca: 667 males and 627 females. Eight ovigerous females were collected in the autumn which corresponds to 2.22% of all adult females. In the Ubatumirim mangrove, during the summer, a total of 2,107 specimens were collected: 1,117 males and 990 females with 20 ovigerous females (3.03%). Most of the ovigerous females collected from both mangroves bore eggs in the final embryonic developmental stage. The additional collection taken in November 2002 comprised 27 ovigerous females from Itamambuca and 67 from Ubatumirim. Most of the ovigerous crabs eggs were in the final developmental stage. When collected, the crabs had emerged from burrows and were moving freely on the substrata. Ovigerous females ranged from 14.2 to 24.2 mm CW at Itamambuca and 10.2 to 21.3 mm CW at Ubatumirim. The mean size of ovigerous females from Itamambuca (19.5 ± 3.3 mm; mean  $\pm s$ ) was larger than ovigerous females from Ubatumirim (16.2  $\pm$  3.2 mm; mean  $\pm$  s) (Student t = test; P < 0.05).

Males with developed gonads were found in all seasons, but significantly more males in this condition were found in the summer and autumn at Itamambuca (P < 0.05) (Table 1). Males with developing gonads were found in all seasons, but significantly more were found in the spring and summer at Ubatumirim (ANOVA; P < 0.05) (Table 2).

Females with developing and developed gonads were found in most of the samples, except during the winter at Ubatumirim. Females with advanced gonads occurred only during the summer at both sites (P < 0.05). In both populations there were many females with spent gonads in the autumn and winter (ANOVA; P < 0.05), unlike in the other seasons (Tables 1 and 2).

In the Itamambuca mangrove, mature males were found in higher frequencies during autumn, spring, and summer, whereas mature females increased only during summer (Table 3) (ANOVA; P < 0.05). At Ubatumirim, mature males were frequent in all seasons of the year, and mature females were frequent during spring and summer (Table 4) (ANOVA; P < 0.05).

The mean air temperature was similar between mangrove sites and did not differ markedly through seasons (ANOVA; P < 0.05). The lower temperatures were registered during autumn (ANOVA; P < 0.05) (Table 5). The mean temperature inside the burrows of *U. rapax* did not

#### TABLE 1

Frequency (%) of the gonad stages (SP = spent; AD = advanced; DE = developed; DI = developing; RU = rudimentary; IM = immature) for male and female *Uca rapax* during the seasons (Au = Autum; W = Winter; Spr = Spring; Su = Summer) in the Itamambuca mangrove.

	Seasons				
Stages	Au	W	Spr	Su	
Males					
SP	17.0 a	18.0 a	15.0 a	15.0 a	
	AB	A	BC	BC	
DE	15.0 a	5.0 bc	0.5 c	12.0 ab	
	С	С	С	BC	
DI	34.0 a	35.0 a	35.0 a	37.0 a	
	A	Α	В	A	
RU	3.0 c	15.0 Ъ	27.0 ab	30.0 a	
	С	BC	AB	AB	
IM	29.0 a	27.0 a	22.0 a	5.0 b	
	AB	AB	AB	С	
Females					
SP	55.0 a	41.0 ab	15.0 c	35.0 b	
	A	Α	В	А	
AD	0.6 b	0.0 b	0.0 Ъ	11.0 a	
	D	BC	С	BC	
DE	2.0 Ь	3.0 c	7.0 a	9.0 a	
	CD	BC	В	BC	
DI	8.0 ab	3.0 b	15.0 a	23.0 a	
	С	BC	В	AB	
RU	2.0 c	6.0 bc	29.0 ab	15.0 a	
	CD	С	Α	BC	
IM	31.0 a	46.0 a	32.0 a	7.0 Ъ	
	В	Α	Α	С	

Note: lower case letters correspond to the comparisons in each gonad stage among the seasons; capital letters correspond to the comparisons among the gonad stages in each season. Values with at least one letter in common did not differ statistically ( $\alpha = 0.05$ ).

differ between sites in a same season but reached maximum values during the summer at both sites (ANOVA; P < 0.05) (Table 5).

The relative frequency of mature males and females tended to increase with increasing air temperature (Itamambuca:  $r^2 = 0.71$  in males;  $r^2 = 0.53$  in females; Ubatumirim:  $r^2 = 0.98$  in males;  $r^2 = 0.66$  in females; P < 0.05) (Figure 1).

Throughout the year, significantly more (ANOVA; P < 0.05) specimens were in the intermolt than molt stages for

#### TABLE 2

Frequency (%) of the gonad stages (SP = spent; AD = advanced; DE = developed; DI = developing; RU = rudimentary; IM = immature) for male and female *Uca rapax* during the seasons (Au = Autum; W = Winter; Spr = Spring; Su = Summer) in the Itamambuca mangrove.

	Seasons			
Stages	Au	W	Spr	Su
Males	***************************************		******	*****
SP	37.0 ab	43.0 a	28.0 bc	24.0 c
	A	А	А	AB
DE	3.0 a	0.7 a	2.0 a	12.0 a
	В	С	С	BC
DI	14.0 Ъ	20.0 Ъ	33.0 a	33.0 a
	С	В	Α	Α
RU	12.0 Ъ	17.0 ab	23.0 a	21.0 ab
	С	В	AB	ABC
IM	33.0 a	20.0 Ъ	13.0 b	10.0 Ъ
	А	В	В	С
Females				
SP	11.0 ab	20.0 a	8.0 b	8.0 b
	В	С	В	В
AD	0.0 a	0.0 a	0.0 a	6.0 b
	С	В	С	в
DE	3.0 ab	0.0 Ь	8.0 a	18.0 a
	C	В	в	BC
DI	6.0 b	0.4 c	28.0 a	19.0 a
	BC	В	А	С
RU	43.0 ab	41.0 a	31.0 b	8.0 c
	Α	A	A	Α
IM	36.0 ab	39.0 a	24.0 b	11.0 c
	Α	A	A	BC

Note: lower case letters correspond to the comparisons in each gonad stage among the seasons; capital letters correspond to the comparisons among the gonad stages in each season. Values with at least one letter in common did not differ statistically ( $\alpha = 0.05$ ).

both populations (Figures 2 and 3). There were no significant differences between sexes in the molt activity, except for males in Itamambuca (Figure 2). Smaller crabs of both sexes molted more often (Figure 4).

Figure 5 shows the frequency of molt activity of U. rapax in relation to gonadal development stages for each sex. The recently molted stage A (see Materials and Methods) was observed in male crabs that had immature gonads and females with immature and rudimentary gonads in the Itamambuca mangrove population. At Ubatumirim,

#### TABLE 3

Frequency (%) of immature and mature *Uca rapax* by season in the Itamambuca mangrove.

Seasons	Males		Females	
	Immature	Mature	Immature	Mature
Autumn	37.7 ab	62.3 a	38.8 b	61.2 b
Winter	50.6 a	49.4 b	61.4 a	38.6 c
Spring	37.0 ab	63.0 a	46.2 b	53.8 b
Summer	35.6 b	64.4 a	21.9 с	78.1 a

Note: lower case letters correspond to the comparison between each demographic category for each sampling season. Values with at least one letter in common did not differ statistically ( $\alpha = 0.05$ ).

#### TABLE 4

Frequency (%) of immature and mature *Uca rapax* by season in the Itamambuca mangrove.

	Males		Females	
Seasons	Immature	Mature	Immature	Mature
Autumn	45.0a	55.0b	79.3a	20.7b
Winter	36.6ab	63.4ab	79.9a	20.1b
Spring	36.8ab	63.2ab	55.5b	44.5a
Summer	31.2b	68.8a	59.5b	40.5a

Note: lower case letters correspond to the comparison between each demographic category in each sampling season. Values with at least one letter in common did not differ statistically ( $\alpha = 0.05$ ).

this molt stage was observed in males with rudimentary and spent gonads, but it was not observed in any females. Male crabs in the post-advanced molt stage (B) have been found in all gonad stages from both mangroves. However, this molt stage was not observed in female crabs with advanced gonads from Itamambuca, or in females with advanced and developed gonads from Ubatumirim.

#### DISCUSSION

In the main systematic sampling period, a small number of ovigerous females were found in Itamambuca and Ubatumirim mangroves. However, additional ovigerous females were collected in the additional samples (August-December 2002), and most of them had emerged from and were moving around the burrows and carrying eggs in the late embryonic stage. According to Salmon (1987), females of broad-fronted fiddler crabs such as *U. rapax* can incubate their eggs underground to protect them from extreme environmental conditions. This provides

#### TABLE 5

		Si	ites	
	Itamambuca		Ubatu	mirim
Seasons	Air temperature	<b>Burrows temperature</b>	Air temperature	<b>Burrow temperature</b>
Autumn	$24.6 \pm 5.36$ b	$25.00 \pm 4.52 \text{ bc}$	$25.00 \pm 1.10$ b	$24.70 \pm 2.15$ b
Winter	$30.10 \pm 6.02$ a	$22.80 \pm 0.79$ c	$28.20 \pm 2.79$ ab	$26.80 \pm 2.53$ b
Spring	31.10 ± 5.76 a	$27.50 \pm 0.91$ bc	$27.80 \pm 2.73$ ab	$25.10 \pm 3.03$ b
Summer	$32.90 \pm 1.78$ a	$31.60 \pm 2.50$ ab	$32.40 \pm 2.91$ a	$31.60 \pm 4.45$ a

Comparison of mean  $(\pm s)$  temperature in °C between year seasons in the mangroves. s = standard deviation.

Note: Values with at least one letter in common within a column did not differ statistically (ANOVA;  $\alpha = 0.05$ ).

a uniform environment, thus promoting synchrony in embryonic development and larval hatching. Christy and Salmon (1984), Murai et al. (1987), and Henmi (2003) also observed such behavior in *Uca pugilator* (Bosc, 1802), *Uca lactea* (DeHaan, 1875), and *Uca perplexa* (H. Milne Edwards, 1837), respectively. The ovigerous females had large broods, remained in their burrows during the entire incubation period, and did not feed during this phase. We infer that the individuals of *U. rapax* in the mangroves studied may have been searching for a hatching area.

To maximize the probability of larval survival, where their eggs are ripe for hatching, many mangrove crabs travel the long distance to the water's edge during the night (Gifford 1962). Only ovigerous females of *U. rapax* with eggs in the final embryonic development stage were found during this study, probably because these females are more active or exit their burrows to liberate the larvae during spring tide periods. Christy (1978) suggested that the synchronization of reproduction with tidal cycles in *Uca* species could be an adaptation to increase the probability that the planktonic larvae are carried back to the adults' environment by tidal currents.

In species of *Uca* with large broods, the females produce more eggs in a single spawn, but they cannot carry eggs continuously. This is probably because of the vulnerability of the large egg masses to stress and desiccation. Females of these species do not feed enough during the incubation period to develop new oocytes internally. On the other hand, species with small broods produce fewer eggs each spawn but can develop broods continuously; their egg mass is protected, and the females can feed during incubation to develop a new brood (Henmi 1989,

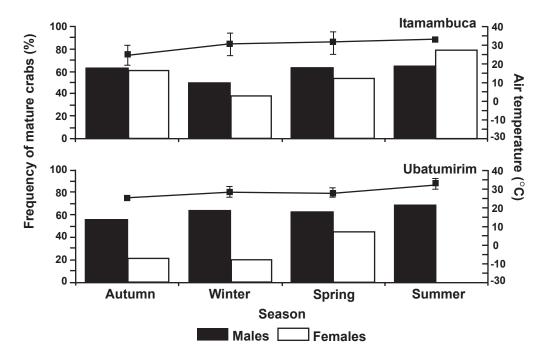
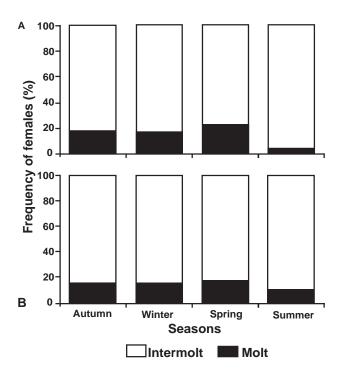


Figure 1. Frequency of mature fiddler crabs (males and females) and air temperature (°C; mean  $\pm s_{\chi}$ ) in both mangroves seasonally.  $s_{\chi}$  = standard error.



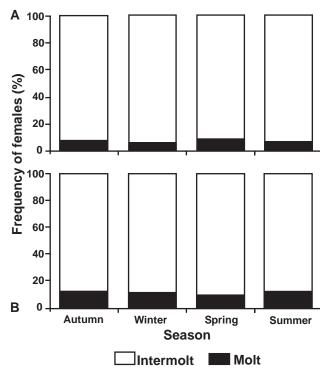


Figure 2. *Uca rapax* in Itamambuca mangrove: Plot of mean seasonal frequency of molt activity and intermolt for males (%) (A), females (B). All seasonal comparisons between molt and intermolt did not differ significantly (P > 0.05).

Henmi and Kaneto 1989). Because the egg mass of *U. rapax* does not remain completely covered by the abdomen, and also because no females were caught with eggs in initial and intermediate embryonic development, we suppose that the ovigerous females remain in their burrows during the incubation period. The ovigerous females collected had spent and empty gonads. These females probably do not bear a new brood immediately after larval hatching as in other *Uca* species as they probably do not feed during the incubation period and have no resources to produce new egg masses.

Fiddler crabs are typically adapted to live in hot climates. In the tropics, they are active year-round, and reproductively active crabs are found during all months, since environmental conditions are permanently favorable for feeding, gonad development, and larval release (Sastry 1983, Thurman 1985). In the subtropics, reproduction in some species is limited more by the dry season than by temperature. For a few species, usually those living in temperate zones, reproduction is controlled by temperature, by their distributional limits, or in some cases by intertidal zonation, e.g., the ocypodid crab *Macrophthalmus grandidieri* A. Milne Edwards, 1867 studied by Emmerson (1994). Reproduction is restricted to the warmer months (summer in the south hemisphere) in fiddler crabs, whereas during the colder months (winter in the south hemisphere)

Figure 3. *Uca rapax* in Ubatumirim mangrove: Plot of mean seasonal frequency of molt activity and intermolt for males (%) (A), females (B). All seasonal comparisons between molt and intermolt did not differ significantly (P > 0.05).

they hibernate in their burrows (Crane 1975). Some investigators (Yamaguchi 1971, Christy 1982, Salmon 1987, Rodríguez et al. 1997) have observed the occurrence of reproduction during warmer months in Uca species. In both mangrove populations that we studied, the period of high reproductive activity in U. rapax occurred in the summer, but this species could also be found reproducing during other months, except in winter. Associations between temperature and reproduction may be related to better conditions for larval development, in terms of the availability of food or more favorable conditions for larval growth. However, in the case of tropical species with year-round procreation, reproduction may be associated with other factors, not only with temperature (Santos and Negreiros-Fransozo 1999, Costa and Negreiros-Fransozo 2003). Factors such as day length, food availability, rainfall and photoperiod have been indicated as other major modulators of reproduction in brachyurans (Conde and Díaz 1989, Zimmerman and Felder 1991, Flores and Negreiros-Fransozo 1998, Leme and Negreiros-Fransozo 1998, Negreiros-Fransozo et al. 2002, Cobo and Fransozo 2003, Litulo 2004).

The *U. rapax* populations of the Itamambuca and Ubatumirim mangroves had high proportions of crabs with developed and advanced gonads during the warmer seasons, which may be related to adequate conditions for

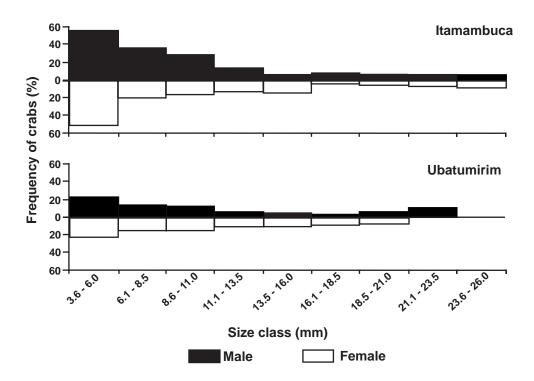


Figure 4. Frequency of molt activity (%) for male and female Uca rapax by size class (carapace width) in both mangroves.

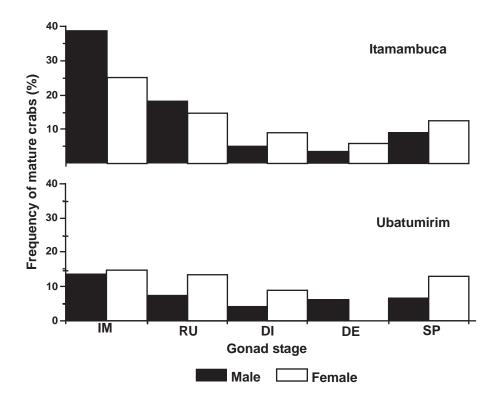


Figure 5. Frequency of molt activity (%) in relation to gonad stages for male and female  $Uca \ rapax$  in both mangroves. IM = immature, RU = rudimentary, DI = developing, DE = developed, and SP = spent.

the development and survival of the brood at these times. Haley (1970), studying the ocypodid Ocypode quadrata (Fabricius 1787) in Texas, observed that females with mature ovaries occurred in high proportions from April to August (spring-summer), suggesting that this period is one of intense reproductive activity. This may be related to day length, which stimulates ovarian maturation in immature females. Negreiros-Fransozo et al. (2002) investigated the biology of O. quadrata in a sandy beach at Ubatuba, Brazil and observed high reproductive intensity from October to May (spring, summer, and autumn). The higher abundance of females with fully developed gonads in this period was positively correlated with abiotic factors such as air temperature, water surface temperature, and precipitation.

The high intensity of molt activity in the first size classes can be explained by the direction of energy into growth until the crabs attain sexual maturity. After this phase, the frequency of the crabs in molt activity decreases, because energy resources become divided between molting and reproduction (Hartnoll 1988). After the pubertal molt, we observed many crabs in the process of molting, which mitigates against the hypothesis that a terminal molt occurs in *U. rapax* soon after sexual maturity.

The low incidence (under 30%) of sexually mature crabs in molt activity is usual for semi-terrestrial crabs. Moreover, fiddler crabs molt underground (Hyatt and Salmon 1978, Christy and Salmon 1984, Salmon 1987, Atkinson and Taylor 1988, Koga et al. 2000).

The antagonism between the reproductive process and growth is well known in crustaceans. The competition for energy resources required by one process or another leads to wide diversity in patterns of growth and reproduction (Hartnoll 1985, López-Greco and Rodríguez 1999). These patterns allow each species to maximize its reproductive potential within the limits of its genotypic plasticity (Hartnoll 1985). It can be assumed that the pattern of *U. rapax* results from the interaction between growth and reproduction. However, several aspects concerning the manner in which these antagonistic processes interact still requires investigation.

In all crustaceans, reproduction is dynamically related to the physical and chemical conditions of the organisms and to environmental conditions, food availability, and the presence of competitors or predators. The relative importance of the proximity of the factors that control reproductive activity can vary for different species in the same environment or in habitats with different characteristics (Sastry 1983). Differences like sediment organic matter content, river and burrow water salinity, and granular composition of the substrate (see Castiglioni and Negreiros-Fransozo 2005) appear to act directly or indirectly on aspects of the populations. Reproduction is especially affected leading to variations in the process in different populations.

This is the first account of the breeding season and molt cycle of *Uca rapax* in Brazil. Further studies on fecundity, fertility, larval migrations, reproductive behavior, and feeding will add to our comprehension of the reproductive strategies of this fiddler crab.

#### **ACKNOWLEDGEMENTS**

We are grateful to the Fundação de Amparo à Pesquisa do Estado de São Paulo-FAPESP, for a fellowship to DSC (#01/01810-9) and financial support for fieldwork to MLNF (98/03134-6). The authors would like to acknowledge C. Tudge for his valuable comments on the manuscript. We also thank the NEBECC staff for their help during field and laboratory activities. All sampling in this study was conducted in compliance with current applicable state and federal laws.

#### LITERATURE CITED

- Abelló, P. 1988. Reproductive biology of *Macropipus tuber-culatus* (Roux, 1830) in the northwestern Mediterranean. Ophelia 30:47-53.
- Atkinson, R.J.A. and A.C. Taylor 1988. Physiological ecology of burrowing decapods. Symposium of the Zoological Society of London 59:201-226.
- Castiglioni, D.S. and M.L. Negreiros-Fransozo. 2004. Comparative analysis of relative growth of *Uca rapax* (Smith) (Crustacea, Ocypodidae) from two mangroves in São Paulo, Brazil. Revista Brasileira de Zoologia 21:137–144.
- Castiglioni, D.S. and M.L. Negreiros-Fransozo. 2005. Comparative population biology of *Uca rapax* (Smith, 1870) (Brachyura, Ocypodidae) from Itamambuca and Ubatumirim mangroves in Ubatuba littoral, Brazil. Journal of Natural History 39:1627–1640.
- Choy, S.C. 1988. Reproductive biology of *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae) from the Gower Peninsula, South Wales. Marine Biology 9:227– 241.
- Christy, J.H. 1978. Adaptive significance of reproductive cycles in the fiddler crab Uca pugilator: A hypothesis. Science 199:453–455.
- Christy, J.H. 1982. Adaptive significance of semi lunar cycles of larval release in fiddler crabs (Genus *Uca*): Test of an hypothesis. Biological Bulletin 163:251-263.
- Christy, J.H. and M. Salmon. 1984. Ecology and evolution of mating systems of fiddler crabs (genus Uca). Biological Review 59:483-509.
- Cobo, V.J. and A. Fransozo. 2003. External factors determining breeding season in the red mangrove crab Goniopsis cruentata (Latreille) (Crustacea, Brachyura, Grapsidae) on the São Paulo State northern coast, Brazil. Revista Brasileira de Zoologia 20:213–217.

- Colpo, K.D. 2001. Biologia populacional comparativa de Uca vocator (Herbst, 1804) (Brachyura, Ocypodidae) em três localidades do litoral norte paulista. M.S. Thesis. Universidade Estadual Paulista-Botucatu, São Paulo, SP, BR, 104 p.
- Colpo, K.D. and M.L. Negreiros-Fransozo. 2003. Reproductive output of Uca vocator (Herbst, 1804) (Brachyura, Ocypodidae) from three subtropical mangroves in Brazil. Crustaceana 76:1-11.
- Conde, J.E. and H. Díaz. 1989. The mangrove tree crab Aratus pisonii in a tropical estuarine coastal region. Estuarine, Coastal and Shelf Science 28:639–650.
- Costa, T.M. and M.L. Negreiros-Fransozo. 1998. The reproductive cycle of *Callinectes danae* Smith, 1869 (Decapoda, Portunidae) in the Ubatuba region, Brazil. Crustaceana 71:615-627.
- Costa, T.M. and M.L. Negreiros-Fransozo. 2003. Population biology of Uca thayeri Rathbun, 1900 (Brachyura, Ocypodidae) in a subtropical South American mangrove area: Results from transect and catch-per-unit-effort techniques. Crustaceana 75:1201–1218.
- Crane, J. 1975. Fiddler crabs of the world. Ocypodidae: Genus Uca. Princeton University Press, Princeton, NJ, USA, 736 p.
- Curi, P.R. and R.V. Moraes. 1981. Associação, homogeneidade e contrastes entre proporções em tabelas contendo distribuições multinomiais. Ciência e Cultura 33:712–722.
- Emmerson, W.D. 1994. Seasonal breeding cycles and sex ratios of eight species of crabs from Mgazana, a mangrove estuary in Transkei, southern Africa. Journal of Crustacean Biology 14:568–578.
- Flores, A.A.V. and M.L. Negreiros-Fransozo. 1998. External factors determining seasonal breeding in a subtropical population of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura: Grapsidae). Invertebrate Reproduction and Development 34:149–155.
- Gifford, C.A. 1962. Some observations on the general biology of the land crab *Cardisoma guanhumi* (Latreille), in South Florida. Biological Bulletin 123:207-223.
- Haefner Jr, P.A. 1976. Distribution, reproduction and moulting of the rock crab, *Cancer irroratus* Say, 1917, in the Mid-Atlantic Bight. Journal of Natural History 10:377–397.
- Haley, S.R. 1970. Reproductive cycling in the ghost crab, Ocypode quadrata (Fabr.) (Brachyura, Ocypodidae). Crustaceana 23:1-11.
- Hartnoll, R.G. 1985. Growth, sexual maturity and reproductive output. In: A.M. Wenner, ed. Factors in Adult Growth. A.A. Balkema, Rotterdam, The Netherlands, 362 p.
- Hartnoll, R.G. 1988. Evolution, systematic and geographical distribution. In: W.W. Burggren and B.R. McMahon, eds. Biology of Land Crabs. Cambridge University Press, Cambridge, UK, 479 p.
- Hartnoll, R.G. and P. Gould. 1988. Brachyuran life history strategies and the optimization of egg production. Symposium of the Zoological Society of London 59:1–9.
- Henmi, Y. 1989. Life-history patterns in two forms of *Macrophthalmus japonicus* (Crustacea: Brachyura). Marine Biology 101:53-60.

- Henmi, Y. 2003. Trade-off between brood size and brood interval and the evolution of underground incubation in three fiddler crabs (*Uca perplexa*, *U. vocans and U. dussumieri*). Journal of Crustacean Biology 23:46–54.
- Henmi, Y. and M. Kaneto. 1989. Reproductive ecology of three ocypodid crabs I. The influence of activity differences on reproductive traits. Ecological Research 4:17–29.
- Hyatt, G.W. and M. Salmon. 1978. Combat in the fiddler crabs Uca pugilator and U. pugnax: A quantitative analysis. Behavior 65:182-211.
- Koga, T., M. Murai, S. Goshima, and S. Poovachiranon. 2000. Underground mating in the fiddler crab Uca tetragon: The association between female life history traits and male mating tactics. Journal of Experimental Marine Biology and Ecology 248:35–52.
- Leme, M.H.A. and M.L. Negreiros-Fransozo. 1998. Reproductive patterns of Aratus pisonii (Decapoda: Grapsidae) from an estuarine area of São Paulo northern coast, Brazil. Revista de Biologia Tropical 46:673–678.
- Litulo, C. 2004. Reproductive aspects of a tropical population of the fiddler crab *Uca annulipes* (H. Milne Edwards, 1837) (Brachyura: Ocypodidae) at Costa do Sol Mangrove, Maputo Bay, southern Mozambique. Hydrobiologia 525:167–173.
- Litulo, C. 2005a. Population structure and reproductive biology of the fiddler crab Uca inversa (Hoffman, 1874) (Brachyura: Ocypodidae). Acta Oecologica 27:135–141.
- Litulo, C. 2005b. Population biology of the fiddler crab Uca annulipes (Brachyura: Ocypodidae) in a tropical East African mangrove (Mozambique). Estuarine, Coastal and Shelf Science 62:283-290.
- López-Greco, L.S. and E.M. Rodríguez. 1999. Annual reproduction and growth of adults crabs *Chasmagnathus granulata* (Crustacea, Brachyura, Grapsidae). Cahiers de Biologie Marine 40:155–164.
- Mantelatto, F.L.M. and A. Fransozo. 1999. Reproductive biology and molting cycle of the crab *Callinectes ornatus* (Decapoda, Portunidae) from the Ubatuba region, São Paulo, Brazil. Crustaceana 72:63–76.
- Melo, G.A.S. 1996. Manual de Identificação dos Brachyura (Caranguejos e Siris) do Litoral Brasileiro. Ed. Plêiade, São Paulo, SP, Brazil, 603 p.
- Moura, D.E., C.C. Lamparelli, F.O. Rodrigues, and R.C. Vincent. 1998. Decomposição de folhas em manguezais na região de Bertioga, São Paulo, Brasil. Proceedings of the IV Simpósio de Ecossistemas Brasileiros 1:130–148.
- Mouton Jr, E.C. and D.L. Felder. 1995. Reproduction of the fiddler crabs Uca longisignalis and Uca spinicarpa in a Gulf of Mexico salt marsh. Estuaries 18:469-481.
- Murai, M., S. Goshima, and Y. Henmi. 1987. Analysis of the mating system of the fiddler crab, Uca lactea. Animal Behavior 35:1334–1342.
- Murai, M., S. Goshima, and Y. Nakasone. 1982. Some behavioral characteristics related to food supply and soil texture of burrowing habitats observed on Uca vocans and U. lactea perplexa. Marine Biology 66:191-197.
- Negreiros-Fransozo, M.L., A. Fransozo, and G. Bertini. 2002. Reproductive cycle and recruitment period of Ocypode quadrata (Decapoda, Ocypodidae) at a sandy beach in southeastern Brazil. Journal of Crustacean Biology 22:157– 161.

- Pillay, K.K. and Y. Ono. 1978. The breeding cycles of two species of grapsid crabs (Crustacea: Decapoda) from the North coast of Kyushu, Japan. Marine Biology 45:273-248.
- Rodriguez, A., P. Drake, and A.M. Arias. 1997. Reproductive periods and larval abundance patterns of the crabs *Panopeus* africanus and Uca tangeri in a shallow inlet (SW Spain). Marine Ecology Progress Series 149:133-142.
- Rosenberg, G.M.S. 2001. The systematics and taxonomy of fiddler crabs: A phylogeny of the genus Uca. Journal of Crustacean Biology 21:839-869.
- Salmon, M. 1987. On the reproductive behavior of the fiddler crab Uca thayeri, with comparisons to U. pugilator and U. vocans: Evidence for behavioral convergence. Journal of Crustacean Biology 7:25-44.
- Santos, S. and M.L. Negreiros-Fransozo. 1999. Reproductive cycle of the swimming crab *Portunus spinimanus* Latreille (Crustacea, Decapoda, Brachyura) from the Ubatuba, São Paulo, Brazil. Revista Brasileira de Zoologia 16:1183– 1193.
- Sastry, A.N. 1983. Ecological aspects of reproduction. In: F.J. Vernberg and W.B. Vernberg, eds. The Biology of Crustacea: Environmental Adaptations, Vol. 8, Academic Press, New York, NY, USA, p. 179–269.

- Schaeffer-Novelli, Y. 1995. Manguezal, Ecosistema entre a Terra e o Mar. Caribbean Ecological Reseach, São Paulo, SP, BR, 64 p.
- Thurman II, C.L. 1985. Reproductive biology and population structure of the fiddler crab Uca subcylindrica (Stimpson). Biological Bulletin 169:215–229.
- Twilley, R.R., S.C. Snedaker, A. Yánez-Arancibia, and E. Medina. 1995. Mangrove systems. In: V.H. Heywood, ed. Global Biodiversity Assessment, Biodiversity and Ecosystem Function: Ecosystem Analyses. Cambridge University Press, Cambridge, UK, p. 387–393.
- Warner, G.F. 1977. The Biology of Crabs. Elek Science, 202 p.
- Wolfrath, B. 1993. Observations on the behaviour of the European fiddler crab Uca tangeri. Marine Ecology Progress Series 100:111–118.
- Yamaguchi, T. 1971. Courtship behavior of a fiddler crab, Uca lactea. Kumamoto Journal of Science Biology 10:13-37.
- Zar, J.H. 1996. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, NJ, USA, 663 p.
- Zimmerman, T.L. and D.L. Felder. 1991. Reproductive ecology of an intertidal brachyuran crab Sesarma sp. (nr. reticulatum), from the Gulf of Mexico. Biological Bulletin 181:387-401.